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"Last Occurrence" of the Antillean Insectivoran *Nesophontes*: New Radiometric Dates and Their Interpretation

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ABSTRACT

Several times during this century it has been claimed on the basis of anecdotal evidence that some of the allegedly extinct endemic mammals of the Greater Antilles still survive in remote areas. To investigate this possibility, an attempt was made in 1996 to locate living representatives of the island-shrew genus *Nesophontes* (Insectivora, Nesophontidae) in the Sierra de Baoruco, Dominican Republic. The attempt was unsuccessful. However, in a related project, it was found that nesophontid remains from Cuba and Hispaniola, judged to be very recent on associational grounds, were in fact much older (12th–15th centuries AD) according to AMS ^{14}C dating. This information, combined with other evidence discussed here, suggests that species of *Nesophontes* may have collapsed extremely rapidly, close to the time of the first European entry into the West Indies. We discovered no direct evidence that predation by or competition with Old World rats or other exotic species caused nesophontid extinctions. Neither recent collecting efforts nor radiometric evidence support the view that any island-shrew species survived into the 20th century.

HOLOCENE LAND-MAMMAL EXTINCTIONS IN THE WEST INDIES

The inventory of terrestrial mammals living in the West Indies during the Quaternary period is incomplete, but 70 to 80 species (omitting Chiroptera) is a reasonable estimate (Varona, 1974; Woods et al., 1985; Morgan and Woods, 1986; authors' unpubl. data). Of these, 75–80% became extinct during the course of the Holocene (Morgan and Woods, 1986; Flemming et al., 1998; Mac-

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TABLE 1
Holocene Land Mammals of Hispaniola (Including Introduced Rodents)

EXTANT ENDEMIC MAMMALS	
Insectivora	*Solenodon paradoxus*
Rodentia	*Plagiodontia aedium*
EXTINCT ENDEMIC MAMMALS	
Insectivora (Soricomorpha)	*Solenodon marcanoi*
	Nesophontes hypomicrus
	Nesophontes micrus
	Nesophontes zamicrus
Xenarthra (Phyllophaga)	*Parocnus serus*
	Synocnus comes
	Unnamed sloth species A[a]
	Unnamed sloth species B[a]
Rodentia (Caviomorpha)	*Hexolobodon phenax*
	Plagiodontia araeum
	Plagiodontia ipnaeum
	Rhizoplagiodontia lemkei
	Isolobodon portoricensis
	Isolobodon montanus
	Brotomys contractus
	Brotomys voratus
	Quemisia gravis
Primates (Platyrrhini)	*Antillothrix bernensis*
INTRODUCED RODENTS	*Rattus rattus*
	Rattus norvegicus
	Mus musculus
	Cavia sp.

[a] See White et al. (1996).

Phee and Flemming, 1999; McFarlane, in press). Virtually all islands with resident land mammals were affected by extinction, some severely: for example, Puerto Rico lost all its native species, while Hispaniola lost 90% of its known complement (18 of 20 species; table 1). In the past 500 years alone, 38% of all mammalian species-level extinctions have taken place on Caribbean islands (MacPhee and Flemming, 1999)—a far higher proportion than that recorded for mainland Australia (19% of global losses), usually regarded as the hardest-hit geographical area on the planet (cf. Flannery, 1994). Although the general magnitude of West Indian losses is not in dispute, there is little agreement concerning their correlation, timing, or causes (MacPhee, 1997).

To place the results reported here in perspective, it is useful to explore briefly what is known or suspected about West Indian extinctions in the Holocene. Our working hypothesis, based on a broad survey of the evidence (MacPhee, 1996, 1997; Flemming et al., 1998), is that the Holocene land-mammal fauna of the West Indies was sharply reduced in two, apparently discrete, episodes. (A third Quaternary episode can be discriminated, but as it occurred during the Last Interglacial it is not relevant to this discussion [Flemming et al., 1998; McFarlane et al., 1998a, 1998b].) The earlier of the two episodes took place in the mid-Holocene and principally affected larger species (e.g., megalonychid sloths, some large-bodied rodents, and platyrrhine primates). Around AD 1500 a second extinction episode began; it was necessarily a microfaunal event, as most Antillean mammals larger than a few kilograms had disappeared long before. These two episodes may have been separated by a lull lasting several thousand years during which few if any extinctions ensued, but this remains to be demonstrated conclusively (MacPhee, 1997).

It should be noted that losses also occurred among Antillean birds and reptiles, but mammals were affected disproportionately (Morgan and Woods, 1986). A similar taxic bias is strikingly obvious in the distribution of vertebrate losses that occurred 11,000 radiocarbon years before present (rcyrbp) on New World mainlands. At that time, approximately 135 mammal species—but only a small number of other vertebrates—died out, perhaps in the space of a few centuries (Graham et al., 1997; Flemming and MacPhee, 1997; MacPhee and Flemming, 1997; Martin and Steadman, 1999). Interestingly, mainland and insular losses in the New World seem to have been decoupled in time, apparently completely. As far as can now be determined, no mammal extinctions occurred in the West Indies in the terminal Pleistocene; perhaps more surprisingly, for the last 10,000 years, none has occurred in the continental parts of the New World either (MacPhee and Flemming, 1997, 1999).[4] Evidently, separate cataclysms require separate explanations.

The two-phase hypothesis of West Indian Holocene extinctions would appear to be

[4] The Omilteme cottontail of central Mexico, *Sylvilagus insonus*, has not been seen since 1991 and is possibly extinct (Cervantes and Lorenzo, 1997).

ready-made to fit the standard interpretation of late Quaternary losses—that they were somehow induced anthropogenically (Martin, 1984; Martin and Steadman, 1999). Certainly, an argument can be made for a broad match between extinction episodes and first appearances of both Amerindians and Europeans in the West Indies. However, many uncertainties remain, as may be seen from a brief exploration of existing "last occurrence" dates for mid-Holocene vertebrate losses. Some "last occurrence" dates correlate well with estimated times for the spread of humans through the Greater Antilles, thought to have begun with Cuba and Hispaniola 6000—7000 years ago (Rouse, 1992; Burney et al., 1994). Thus for Cuba, the latest acceptable ^{14}C date for megalonychid sloths is 6250 ± 50 rcyrbp (unpubl. data on *Megalocnus rodens* from Cueva Beruvides, Matanzas; see fig. 1), in apparently good agreement with the trend of the earliest archeological dates for this island (Burney et al., 1994). In the case of Hispaniola, however, the latest reported date is almost 2500 years later, at 3755 ± 175 rcyrbp (Woods, 1989; unspecified sloth remains from Trou Woch Sa Wo, Tiburon Peninsula, Haiti; see fig. 1). Much younger dates have been claimed for Cuban specimens dated by nonradiometric methods (Suarez et al., 1984; Pino and Castellanos, 1985), and there are even some anecdotal reports alleging megafaunal survival well into the present century (Woods et al., 1985). The veracity of this information is impossible to confirm or disconfirm (see discussions by MacPhee and Marx, 1997).

As is very often the case when one looks for hard evidence of direct human complicity in late Quaternary extinctions, there isn't much to be found (MacPhee and Marx, 1997). Despite persistent claims to the contrary (e.g., Harrington, 1921; Suarez et al., 1984; Pino and Castellanos, 1985), no convincing evidence of human/megafaunal interactions, in the form of kill sites, food detritus, or worked bone, has ever turned up in any Caribbean context. In marked contrast, ample evidence exists of human utilization of smaller endemic mammals, indicating that Amerindians were certainly interested in exploiting this resource (J. A. Allen, 1916; Miller, 1929a, 1929b; Pregill et al., 1994; Wing, 1995; Flemming and MacPhee, in prep.). Although such information can hardly be considered conclusive, the absence of evidence for megafaunal exploitation on the islands is best explained by assuming that larger species disappeared at or very shortly after the beginning of human tenure.

The pattern of losses is usually thought to be more clear-cut for the modern era (i.e., post-1500). For various reasons (cf. Woods et al., 1985), it has been generally accepted that the modern-era pattern has been one of rather gradual loss, with many species hanging on long after 1500 until they were finally removed by one calamity or another (e.g., habitat destruction, introduction of exotics). However, the evidence for gradual loss is actually thin and inadequately examined. Because the majority of Antillean species believed to have become extinct in the modern era were never described by literate humans, extinction times can be determined only by using criteria other than direct observation. The criterion most widely utilized is co-occurrence, in apparently undisturbed contexts, of the remains of now-extinct endemics with those of exotic species (usually Old World rats) (e.g., Miller, 1929a, 1929b; G. M. Allen, 1942; Woods et al., 1985). However, as a chronometric tool, exotic associations must be regarded as a rather blunt instrument. Of 33 instances of modern-era species-level extinctions in the West Indies accepted by MacPhee and Flemming (1999), only six (18%) can be given effective extinction dates (EEDs) in calendar years, no one of which predates 1881. EEDs for the remaining 82% cannot be constrained more narrowly than to state that they occurred at some unspecifiable time "since AD 1500" (i.e., the accepted proxy date for the introduction of *Rattus rattus* into the West Indies).

Why is it important to know when a species died out? Explaining cause/effect relationships is one obvious reason (Caughley and Gunn, 1996). Without some sense of the order of events, mechanisms of extinction cannot be resolved meaningfully. Some extinction theories, such as the hyperdisease hypothesis of MacPhee and Marx (1997), stipulate that the majority of losses, especially ones occurring in island settings,

should take place soon after the appearance of the precipitating cause, i.e., on a decadal scale. Other theories (e.g., various "climate change" hypotheses) permit much longer intervals between the appearance of the cause and the production of its effect, that is, on a centennial or millennial scale. Although some historical extinctions on islands are known to have been swift and sudden, in other cases the period of loss was evidently protracted (Martin and Steadman, 1999), indicating that human impacts may vary substantially depending on the life history and autecology of the species affected.

Has the majority of modern-era mammal losses in the West Indies occurred quickly or slowly, and how can we tell the difference? A large quantity of baseline chronometric data, by species and by island, will have to be collected before this question can be answered usefully (MacPhee et al., 1989; McFarlane, 1999). In this paper we contribute to the needed database by evaluating new "last occurrence" dates for island-shrews, members of the endemic Antillean insectivoran genus *Nesophontes* (table 2). *Nesophontes*, with 11 species extinct and none extant, is one of two late Cenozoic insectivoran genera known from the Greater Antilles (cf. MacPhee and Grimaldi, 1996). The other genus, *Solenodon,* is represented by two extant and two extinct species (Morgan and Ottenwalder, 1993). (Dr. H. P. Whidden [personal commun.] is currently revising Nesophontidae; pending publication of his results, we will continue to accept existing nomina and species' limits.)

TABLE 2
Known Ranges of Nominal Species of *Nesophontes*

Taxon	Range[a]
Nesophontes edithae	Puerto Rico, Vieques, St. Johns, St. Thomas
Nesophontes hypomicrus	Hispaniola, Gonave Island
Nesophontes longirostris	Cuba
Nesophontes major	Cuba
Nesophontes micrus	Cuba, Isle of Pines, Hispaniola
Nesophontes paramicrus	Hispaniola
Nesophontes submicrus	Cuba
Nesophontes superstes	Cuba
Nesophontes zamicrus	Hispaniola
Nesophontes sp. 1[b]	Grand Cayman
Nesophontes sp. 2[b]	Cayman Brac

[a] See figure 1.
[b] See Morgan (1994).

There are several reasons for choosing to date island-shrews, but three are paramount. First, *Nesophontes* is of particular importance for the study of West Indian extinctions because this genus, despite its extensive radiation and wide geographical distribution, lost its entire standing diversity in the Quaternary (table 2). Secondly, "hard" EEDs for species of *Nesophontes* are unavailable, as no island-shrew was collected in the living state or described recognizably by early chroniclers (e.g., Oviedo y Valdés, 1535). Thirdly, it has long been accepted that one or more species of this genus survived well into the modern era, perhaps even into the first decades of the present century (e.g., Woods et al., 1985; Balouet and Alibert, 1990).

This last point is of special significance. A number of investigators have reported discovering remains of *Nesophontes* commingled with those of *Rattus rattus* at the same stratigraphic level in excavated sites or in surface assemblages. By far the most intriguing of these associations was reported by Miller (1930), who described unusually well-preserved owl-pellet material from a site in south-central Hispaniola (see Methods). This material included *Nesophontes paramicrus* and several other extinct Hispaniolan endemics in undoubted physical association with *R. rattus* and—unexpectedly—quantities of hair and pieces of dried soft tissues adherent to many of the bones. Miller's (1930: 6) rather breathless conclusion, that the bones "have the appearance of such freshness that it is easy to believe that they were dropped by the owls within a period not greater than a year or two before," has since become the essential basis for the argument that some island-shrews survived very late, perhaps even into the 1930s (e.g., G. M. Allen, 1942; Balouet and Alibert, 1990; Woods et al., 1985).

In assessing these points, it is useful to explore several features of the nesophontid extinctions in a wider perspective. First, it is important to note that virtually all insectivoran families have managed to avoid extinctions at the species level during the past 500 years. Indeed, with the exception of one

extinct species of *Solenodon*, all modern-era losses in Order Insectivora have occurred in just one family, Nesophontidae. (We acknowledge that several species of the soricid *Soriculus* [= *Nesiotites*] have recently disappeared from islands in the western Mediterranean, but according to the available evidence these losses occurred during Roman times and earlier [Vigne, 1992]). By contrast, Afro-Malagasy tenrecids—in some ways the ecological vicars of Antillean insectivorans and therefore of comparative interest here (Eisenberg and Gould, 1970; Woods and Eisenberg, 1989)—have not suffered a single species-level extinction in the late Holocene, although at least two dozen other Malagasy vertebrates died out during this interval (Burney and MacPhee, 1988; MacPhee and Flemming, 1999).

Secondly, the total eradication of family Nesophontidae implies an unusually severe selective regime, but one that was nevertheless locally variable. If Miller's (1930) interpretation is valid, there had to have been some contexts in which extinction pressures on *Nesophontes* species were reduced or absent, permitting their survival into very recent times. Woods et al. (1985) argued that *Nesophontes*, as well as some of the endemic rodents now believed extinct, may have been able to hold out in highland regions of Hispaniola long after the introduction of rats and mice to the island, only to succumb after the introduction of mongooses in the 1870s (Hoagland et al., 1989). To test their argument, Woods and co-workers investigated likely areas in Haiti, Dominican Republic, and Puerto Rico, but they were unsuccessful in securing any physical evidence of late survival of extinct endemic mammals.

Thirdly, the evidence for *Nesophontes*/*Rattus* associations is rarely robust and the documentation provided by investigators is usually minimal, which makes associational claims difficult to assess. In a typical chain of inference, Fischer (1977) stated that material of *N. superstes*, a Cuban species, was recovered in association with fresh-looking remains of *Rattus*, and on this basis he speculated that *superstes* might still be extant. However, the nature of the association was not made clear or tested by some other means (e.g., radiocarbon dating). A more cautious approach is exemplified by Koopman and Ruibal (1955: 7), who found remains of *N. micrus* in caves in Camagüey in which *Rattus* and *Mus* bones also occurred. They stated that "[n]one of the material was stratified, all of it having been intermixed by the diggings for bat guano. It is therefore impossible to establish the relative age of the fossils." It should also be appreciated that associational evidence does not exist in any form for some species. To date, *Nesophontes*/*Rattus* associations have been reported for seven species: *N. hypomicrus*, *micrus*, *paramicrus*, *superstes*, *zamicrus*, plus two unnamed island-shrews from Cayman Islands. Associations have yet to be reported for *N. edithae*, *submicrus*, *major*, and *longirostris*, which means that their EED status is quite uncertain (see MacPhee and Flemming, 1999).[5]

In summary, there is much uncertainty concerning when island-shrew species actually became extinct and whether they disappeared in correlation with the appearance of a specific common cause. The purpose of our research, described below, was (1) to ascertain whether any island-shrew species still existed on the island of Hispaniola, by using several trapping techniques; and (2) to better resolve EEDs of various nesophontids by radiometrically dating remains recovered from crucial contexts.

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[5] Puerto Rican *N. edithae* may have died out much earlier than AD 1500, although this needs to be confirmed. The youngest date on record, 5410 ± 80 rcyrbp (McFarlane, 1999), is actually for avian material found in association with remains of *edithae*.

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Abbreviations

AMNH	American Museum of Natural History
AMS ^{14}C	accelerator mass spectrometry radiocarbon dating
Beta	Beta Analytic, Coral Gables, FL (radiocarbon dating lab)
cal-AD	solar years AD (used with calibrated dates)
EED	effective extinction date
rcyrbp	radiocarbon years before present (radiometric datum, AD 1950)
USNM	United States National Museum of Natural History

Methods

As part of a project designed to determine whether any of the putatively extinct endemic mammal species of Hispaniola still survive on that island, in May 1996, we conducted a survey of likely habitats in the isolated Parque Nacional Sierra de Baoruco in southwestern Dominican Republic. Our strategy had two components: one was to set pitfall, live, and snap traps in various locales to ascertain whether any of the target species might be captured directly; the other was to prospect in cave sites for fresh-looking material for radiometric dating. In this paper we report new ^{14}C records for fossil specimens of *Nesophontes* collected by ourselves and by others and consider their significance for adjudicating the extinction dates of species known exclusively from fossil evidence (for additional discussion of procedures for estimating EEDs, see MacPhee and Flemming [1999]).

Neontological collecting was conducted as an experiment only, to see whether more intensive trapping was warranted. The results were extremely sparse (*Rattus rattus* was the only mammal collected), but relevant to the degree that no allegedly extinct species were recovered. Results and techniques are discussed briefly under the entry "Cueva Jurg" (see below) and in the footnotes accompanying table 4.

Constanza Collections

In the spring of 1930, Herbert W. Krieger, then making anthropological collections for the USNM, worked for several weeks at cave sites in Haiti and Dominican Republic collecting vertebrate fossils. The mammalian material that he recovered was described by Miller (1930). Of importance here are Krieger's collections made at the localities here referred to as the Cerro de Monte Indian Site and the Monte Culo de Maco Shelter Site, both near the town of Constanza in south-central Dominican Republic (fig. 1). Remains of extinct mammals were found at both sites (table 3). Fortunately, Miller curated and described the Constanza collections in considerable detail. Although only a fraction of the specimens were accessioned formally into the USNM collections, it is possible to assign critical specimens to either Cerro de Monte or Monte Culo de Maco using Miller's notes.

Of several Amerindian midden sites excavated by Krieger near Constanza, Cerro de Monte, located 6 km east of town, was the only one that yielded a significant number of species (table 3). Although no Spanish-era artifacts were encountered, remains of a colt, several pigs, and *Rattus rattus* were recovered in addition to a few bones of endemic species. There is no indication that the site (described as being 2.5 ft deep) was dug stratigraphically; associations between extinct Antillean mammals and other taxa, if any, were therefore lost at the time of excavation. In view of the possibility of disturbance we decided that it would not be cost effective to date specimens from this site.

The Monte Culo de Maco site was described by Miller (1930) on the basis of Krieger's notes as a shelter formed by an over-

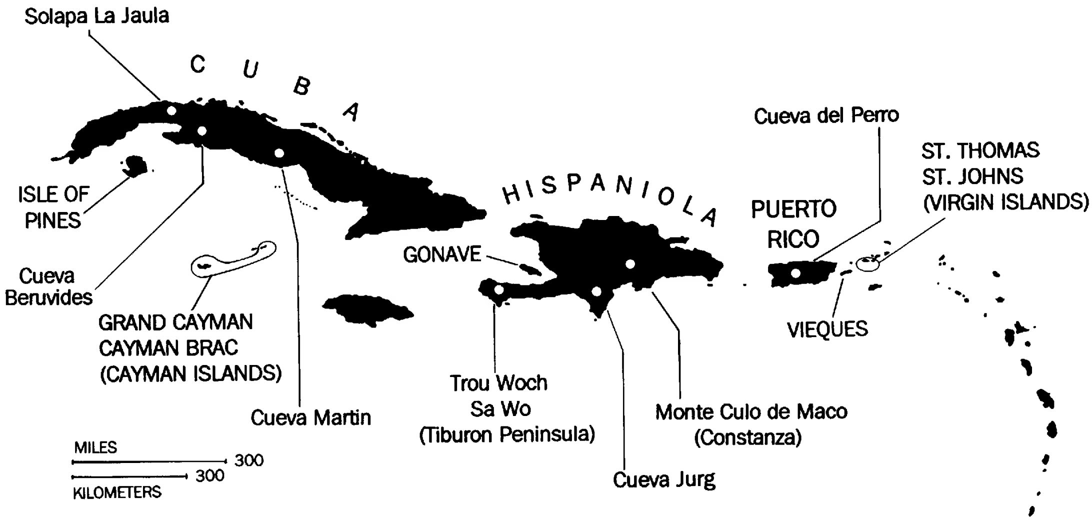

Fig. 1. Sketch map of the West Indies, identifying places mentioned in the text. Sites that have associated radiocarbon dates are highlighted by white dots. Only islands that supported *Nesophontes* species are named (in case of St. Thomas and St. Johns, evidence is archeological; Woods [1996]).

hanging ledge, situated about 100 ft above the Arroyo Limoncillo, on the northern flank of Monte Culo de Maco, 10 km southwest of Constanza. Despite this information we were not able to confirm the location of this site in 1996. The material recovered included the remains of several extinct small mammals as well as *Rattus rattus* (table 3). Miller (1930) concluded that the bones had been deposited as vomitus (owl pellets) in the very recent past, and noted their exceptional degree of preservation (see fig. 2):

> One of the femurs, for instance, retains a patch of dried tissue on the anterior basal portion of the greater trochanter and a loose web of hairs in the digital fossa and concave inner aspect of the greater trochanter. The braincase is packed full of hair by the action of the owl's stomach, and the broken anterior part of a skull gives similar evidence of recent submission to digestive action. Most of the jaws have hairs adhering to the teeth or in the spaces between the roots. One has a felt-like mass plastered against the inner side of the ascending ramus.

Miller (1930) identified three nesophontid species (*N. paramicrus*, *N. zamicrus*, and *N. hypomicrus*) in the Monte Culo de Maco collection; we selected three limb bones identified as *N. paramicrus* for radiometric dating (fig. 3).

In order to test for contemporaneity of extinct species with introduced ones, we also dated specimens of *Rattus rattus* from the same USNM collection. For sample comparability we used femora only, but we purposely selected specimens whose physical appearance differed, due to staining and weathering, to increase the chance of recovering the spectrum of time represented by the collection. We submitted three femora for dating, requesting that each be dated at a different AMS facility. Our hypothesis was that, within the usual parameters of experimental and interlab error, all three femora should be the same age if they derived from the pellets produced by a single owl. A wide spread of

TABLE 3
Krieger's Localities Near Constanza: Species Lists (after Miller, 1930)

Cerro de Monte (Indian Site)	Monte Culo de Maco (Shelter Site)
†*Nesophontes paramicrus*	†*Nesophontes paramicrus*
†*Brotomys voratus*	†*Nesophontes hypomicrus*
†*Isolobodon portoricensis*	†*Nesophontes zamicrus*
(incl. *I. levir*)	†*Brotomys voratus*
Plagiodontia aedium	†*Isolobodon* sp.
(incl. *P. hylaeum*)	*Rattus rattus*
Cavia porcellus	*Phyllops falcatus*
Rattus rattus	(incl. *P. haitiensis*)
Sus scrofa	*Eptesicus fuscus*
Equus caballus	(incl. *E. hispaniolae*)

†, extinct species.

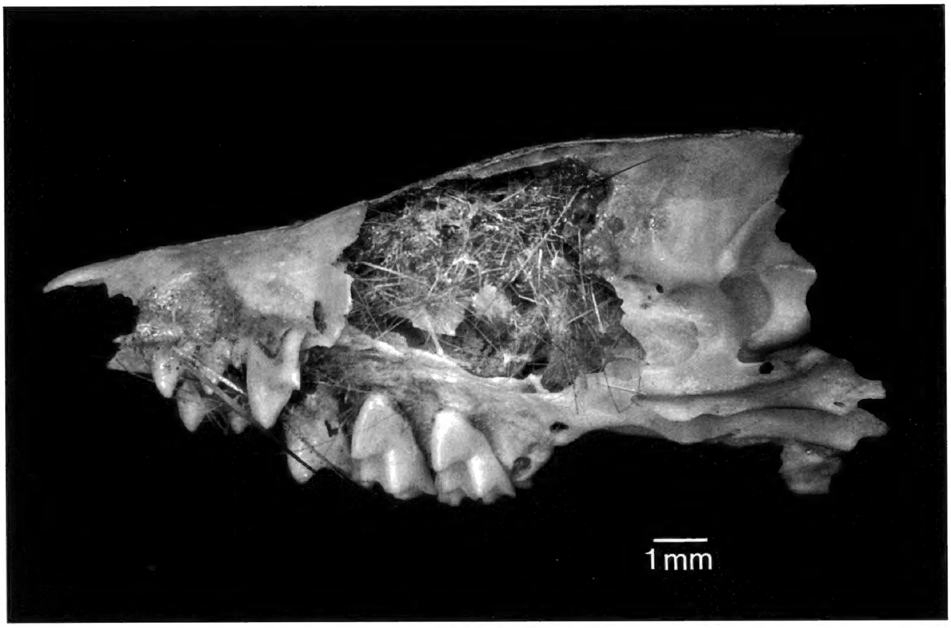

Fig. 2. Skull of *Nesophontes paramicrus* (USNM 255301) collected from owl-pellet deposit at Monte Culo de Maco, near Constanza, Dominican Republic, in 1930 by H. W. Krieger. Note felted hair mass filling cranial cavity. Miller (1930) regarded presence of preserved hair in this and other specimens as evidence that *Nesophontes* survived until very recently, perhaps even into 20th century.

ages would indicate that more than one owl was responsible for the Monte Culo de Maco bone deposit.

Several morphologically different kinds of hair from the owl-pellet material (as seen in fig. 2) can be discriminated in SEM micrographs (illustrated in fig. 4). Although we made no effort to resolve which, if any, belong to *Nesophontes*, we illustrate representative hairs here to encourage their study.

Cueva Jurg and Other Sites

As noted above, the authors undertook an exploratory study in Parque Nacional Sierra de Baoruco to determine whether presumably extinct species of Hispaniolan mammals might still survive in little-disturbed habitat. Pitfall traplines and conventional traps were utilized in pine forest, broadleaf forest, and grassy clearings in various places within the park over a 10-day period (fig. 5). Overall recovery of vertebrates was very meager and does not warrant much comment (table 4). *Rattus rattus* was recovered in all traplines. Although both *Solenodon paradoxus* and *Plagiodontia aedium* are known to exist within the park, neither of these species was encountered in the living state.

The authors also prospected in limestone areas in the park in order to search for owl pellets and other bone accumulations in caves and overhangs. Cueva Jurg proved the most productive paleontological site discovered on this trip (fig. 1). Cueva Jurg is actually a small pocket (~2 m deep, 1 m high) located within the area known locally as Cuevas de la Olla (fig. 6). It is situated about an hour's walk from the ranger's hut located approximately 63 km by road NE of Pedernales, at an altitude of ~1300 m. The floor of Cueva Jurg, widely exposed to the exterior and nearly sediment-free, produced a large number of mammal and herpetological remains in a thin litter. Mammal remains visible on entry included fresh-looking bones of *Nesophontes* and *Rattus*. To insure good recovery, the entire mass of detritus on the floor was collected for later sifting and study in the lab. Among numerous remains of *Nesophontes hypomicrus* were two hemimandibles with small pieces of soft tissues attached (fig. 7). These two specimens (and a

Fig. 3. One of the long bones used for AMS ^{14}C dating (see text and table 5), this tibio-fibula of *Nesophontes paramicrus* (USNM 255780) from Monte Culo de Maco exhibited adherent hair shafts (arrows) and other tissue debris.

third *hypomicrus* hemimandible from the same collection, added to increase sample size) were submitted for dating (see Results).

Two other small collections were made, at Dead Owl Cliff in the Cuevas de la Olla area, and Roadside Overhang, a small shelter near Constanza (table 4). Neither produced remains of identifiably extinct mammals and will not be further described here.

CUBAN SITES

To increase island and species representation for this study, we requested that Cuban colleagues submit nesophontid material to us for radiometric dating. Two skulls of *Nesophontes micrus* from Cueva Martin, Sierra de Escambray, were supplied by Abel Hernandez, then director of the natural history museum in Sancti Spíritus. Skull fragments of the same species, from the site of Solapa La Jaula, near the Escaleras de Jaruco (fig. 1), were collected by Stephen Díaz Franco of the Museo Nacional de Historia Natural, La Habana. In both instances, the specimens were found at surface and unweathered. No associations with hair or rats were noted. These specimens were also submitted for dating (see Results).

RESULTS

AMS ^{14}C dating results for the Hispaniolan and Cuban samples described in the preceding section are reported in tables 5 and 6. No preparation difficulties were noted by the labs performing the work. Measured ^{14}C ages have been corrected to "conventional" ^{14}C ages using the standard $-25‰$ $\partial^{13}C$ correction. Calibrated age intercepts in calendar (cal) year for the conventional ^{14}C dates are provided, together with cal age ranges corresponding to ± 1-sigma (68% probability) and 2-sigma (95% probability) measurement errors.

A number of factors affect the cosmogenic flux of ^{14}C formation; analytically, these factors produce deviations between computed ^{14}C ages and actual ages in solar years (Geyh and Schleicher, 1990). In general, the size of the deviation increases with solar age, but in a nonlinear manner. For dates falling within the last 2000 years, the chronometrician's rule of thumb is that conventional ^{14}C and

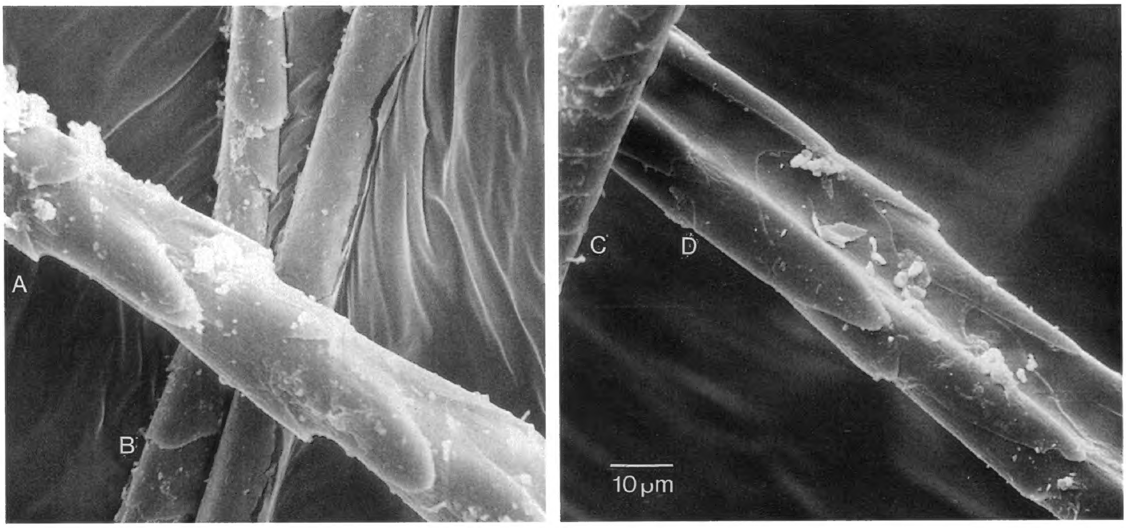

Fig. 4. Selection of scanning electron micrographs of representative hair shafts recovered from cranial cavity of USNM 255301 (see fig. 2). Although these hairs have not been assigned to taxa, they express several obvious morphological contrasts: e.g., shaft cylindrical (A–C) vs. deeply grooved (D); coronal scales slightly divaricated (A, D) vs. tightly appressed (B, C); scale margins entire and sinuous (B, C) vs. margins deeply scalloped or asymmetrical (A, D); successive scales broadly imbricated (A, B, D) vs. narrowly imbricated (C).

actual ages may differ by ± 200 years. Radiocarbon labs correct for this effect routinely, by calibrating dates against internationally accepted calibration curves. However, there are still several sources of uncertainty that are hard to rate for a particular time, place, and material unless extensive prior studies have been conducted. Here we will simply note that, inasmuch as the diets of island-shrews were probably 100% terrestrially derived, "old carbon" reservoir effects are unlikely to affect age determinations to any important degree (see Geyh and Schleicher, 1990).

NESOPHONTES DATES

Calibrated dates (± 1 sigma) for the *Nesophontes* samples from Cuba and Hispaniola range from late 12th to earliest 15th centuries (table 5). Prima facie, these results seem quite plausible: specimens were selected deliberately from surface contexts, and therefore ought to date to comparatively recent times. However, our original expectation was that at least some dates would place well into the 19th or even the 20th centuries, in line with Miller's (1930) hypothesis of late survival. Strikingly, however, none of the dates verges on the present, even at the 2-sigma level. As mentioned above, it is not considered probable that any known reservoir effects would act to increase the radiocarbon ages of small insectivores living in the northern humid tropics. Although the number of dates is small, the selection of material for dating was nonrandom (i.e., was biased toward the most recent contexts). Accordingly, we conclude that there is no inherent problem with the dates themselves.

Instead, it is much more likely that Miller's (1930) proxy indicators of very recent deposition (e.g., hair, soft tissue associations) are untrustworthy. It is now known that under a wide range of conditions hair preserves nearly as well as bone, wood, and many other resilient materials encountered regularly in paleontological and archeological localities (R. Bonnichsen, personal commun.). How long hair and adherent soft tissues might last under tropical conditions is open to question; the *Nesophontes* materials from Monte Culo de Maco and Cueva Jurg were recovered in protected settings in the relatively cool highlands, which may have helped to preserve them. Whatever the specific explanation might be in this case, the important point is

that the occurrence of hair or soft tissue in a depositional context need not be indicative of extremely recent deposition. "Freshness" is evidently not a quality that translates reliably into a specific slice of time.

RATTUS DATES

In contrast to the *Nesophontes* determinations, calibrated dates at ± 1 sigma for the Monte Culo de Maco samples of *Rattus rattus* are later, ranging between the early 15th and mid-17th centuries (table 6). As may be seen by comparing tables 5 and 6, dated *N. paramicrus* material overlaps the lower end of the 2-sigma range for *R. rattus* at Monte Culo de Maco, but only just.

On this evidence it might be permissible to argue that the dated island-shrew and rat bones are effectively contemporaneous, despite the weak overlap. However, this conclusion must be evaluated more critically. The overlap is restricted to the very beginning of the 15th century; that it exists at all results from the remarkably early intercept date (cal-AD 1435) for one *Rattus* sample. This particular calibration has a complex probability distribution which extends (at 2 sigmas) into the 16th and 17th centuries and thus also overlaps the intercept dates of the other two rat samples. Keeping in mind that ranges with lower probability may nevertheless contain true ages, these facts might be harmonized by concluding that all the rat femora may be as late as the 16th or 17th centuries. In that case their apparent "association" with the *Nesophontes paramicrus* material (which is probably no later than the 13th or 14th centuries) would be judged fortuitous, due to a negligible rate of deposition at Cueva Jurg.

Arguably, additional dates might help to resolve this matter. However, as no way of making a preliminary sortation of older versus younger specimens suggested itself, given the small size and limited number of specimens it was decided that additional dating efforts using the same collection would not be cost effective. It may also be noted that, if the interpretation advocated here is accepted, more than one owl had to be involved in creating the bone deposit collected by Krieger at the Monte Culo de Maco shelter.

DISCUSSION

Are all island-shrew species extinct? This question cannot be answered definitively by negative evidence alone. However, it is important that collecting expeditions mounted in the last two decades (Woods et al., 1985; this paper) failed to turn up any indication that *Nesophontes*—or, for that matter, any of the other Hispaniolan mammals on extinction lists—continues to survive. True, these surveys (including our own) have been cursory, and there is certainly a need for more intensive work even if it now seems unlikely that any surviving nesophontid populations remain to be discovered. Cuba, for example, has not been sampled using modern methods, and it is certainly large enough to warrant a try.

Did any island-shrew species survive into the present century? Although there is no reason to suspect that the nesophontid populations sampled at Monte de Culo were the last of their kind, the owl-pellet material from this site was expected to yield evidence of very recent survival of *Nesophontes*. It did not. Specimens from other apparently recent contexts in Cuba and Hispaniola yielded similar results. Looked at objectively, there is no direct radiometric evidence at present that any species of *Nesophontes* even outlasted the close of the 15th century, let alone that of the 19th.

Although presence of well-preserved hair at the Monte Culo de Maco locality is interesting, as a dating tool it is of little or no value. The dates for Monte Culo de Maco establish that hair can be preserved under favorable conditions for many centuries, even in the tropics.

Were introduced species responsible for causing the extinctions of island-shrews? This is a crucial question, as it is widely accepted that the demise of the nesophontids must be connected in some way with the introduction of rats and other Old World exotics around AD 1500 (e.g., G. M. Allen, 1942; Woods et al., 1985). Excessive competition and predation are easy to assume but difficult to demonstrate in cases in which the only evidence necessarily comes from paleontology (cf. Caughley and Gunn, 1996).

Yet it must be more than coincidental that

Fig. 5. Trapline 2 in Sierra de Baoruco set 3 km from camp in moist broadleaf forest (see table 4). In foreground, plastic drift fence spans several buckets buried up to their rims.

many if not all species of island-shrews should have disappeared virtually on the eve of the accepted date of European entry into the New World. Nesophontid remains have been found at every altitudinal setting within their former ranges in the northern Greater Antilles, from montane to coastal plains. Although the point is hard to argue in the absence of adequate vegetational histories for these islands (cf. Burney et al., 1994), it

Fig. 6. View of some of the caves in the area known as Cuevas de la Olla, Sierra de Baoruco (southwestern Dominican Republic).

Fig. 7. Two hemimandibles of *Nesophontes hypomicrus* from Cueva Jurg, Sierra de Baoruco (southwestern Dominican Republic) utilized for AMS ^{14}C dating. **Top,** arrow points to flap of tissue adhering to mandibular ramus posterior to m3. **Bottom,** arrow points to ?gum tissue adherent to base of m3 crown.

seems unlikely that all island-shrew species lived in dense, humid forest. Indeed, recovery of *Nesophontes* bones in Haiti and Dominican Republic, at sites distributed from high-altitude *Pinus* forest to dry coastal plain (Ottenwalder, 1991), indicates that the environmental tolerance of these insectivorans was wide rather than narrow.

Two explanations of the evidence presented here might be considered. One is that, contra Miller (1930) and most other investigators, the demise of the nesophontids may have been acutely swift rather than protracted. Nothing in the still-insubstantial dating record contradicts this conclusion. Indeed, it is interesting to speculate what inference one

TABLE 4
Vertebrates Collected in Sierra de Baoruco, Dominican Republic, May 1996

Class	Taxon	Common name	Neontological collection[a]	Paleontological collection
Amphibia	*Eleutherodactylus* sp.	tree frog	P, S	—
Reptilia	*Anolis cybotes*	anole	G, P	—
	Anolis sp.	anole	—	Cueva Jurg
	Wetmorena haetiana	galliwasp	P	—
	Epicrates sp.	boid snake	—	Cueva Jurg
Aves	*Gallus gallus*	chicken	T	—
	Tyto alba[b]	barn owl	—	Dead Owl Cliff
	Carduelis dominicensis	Antillean siskin	G	—
Mammalia	*Nesophontes hypomicrus*	island-shrew	—	Cueva Jurg
	Nesophontes zamicrus	island-shrew	—	Cueva Jurg
	Solenodon marcanoi	Marcano's solenodon	—	Cueva Jurg
	Rattus rattus	black rat	M, T, V	Cueva Jurg, Roadside Overhang
	Mus musculus	house mouse	—	Roadside Overhang
	Brotomys sp.	esculent mouse	—	Cueva Jurg
	Isolobodon sp.	extinct hutia	—	Cueva Jurg
	capromyid indet.	hutia	—	Cueva Jurg, Roadside Overhang
	Monophyllus redmani	Jamaican long-tongued bat	—	Cueva Jurg
	Eptesicus fuscus	big brown bat	—	Cueva Jurg, Dead Owl Cliff

[a] Summary of trapping activities: 4 traplines were set, consisting of pitfall and conventional traps (latter including folding Tomahawk live traps, folding aluminum Sherman live traps, Victor Holdfast snap traps, Museum Special snap traps, No. 110 Conibear traps, and one glue trap). Conventional traps were baited with a mix of 50% peanut butter, 22% oatmeal, 22% raisins, 5% bacon, with splash of vanilla extract added just prior to field use. Key: G, glue; M, Museum Special snap; P, pitfall; S, Sherman live; T, Tomahawk live; V, Victor snap.

Each pitfall trapline consisted of 11 16-liter buckets, sunk flush with ground and placed at 5-m intervals in a more or less straight line, connected by a plastic drift fence as illustrated in figure 5. Total for all 4 pitfall traplines = 297 bucket-nights.

Trapline 1 set 0.5 km from camp in pine/fern habitat, in a clearing near water cistern. In addition to pitfall line, we set 11 Victors, 25 Shermans, 1 Tomahawk for a total of 111 trap nights. Mammals collected: 8 *Rattus rattus* in snap traps. Several feral chicks in Tomahawks. No vertebrate yield from pitfall line.

Traplines 2 and 3 set 3 km from camp in moist broadleaf forest. Trapline 2 ran up a gently sloping hill; Trapline 3 placed along a nearby pond in setting of broadleaf trees, treeferns, ground ferns, bamboo, and a few scattered pines. Rotten logs abounded, light level low, humid. In addition to pitfall lines, we set 31 Victors, 25 Shermans, 6 Tomahawks for a total of 350 trap nights. Mammals collected: 10 *Rattus rattus* in Victors, 1 in Tomahawk (released). Shermans caught frogs only. Pitfall traplines caught frogs, lizards, and invertebrates.

Trapline 4 set 10.6 km from camp, in an open grassy clearing with occasional *Pinus occidentalis* and numerous burned-out stumps, fronted by limestone ridge; area damp and misty. In addition to pitfall line, we set along the ridge 11 Victors, 20 Museum Specials, 4 Tomahawks and 1 glue for a total of 222 trap nights. Mammals collected: 1 *Rattus rattus* in Victor. *Eleutherodactylus, Anolis, Wetmorena* in pitfall trapline; *Carduelis dominicensis* in glue (released).

[b] Fresh dead specimen.

might have reached about island-shrew extinctions if only the *Rattus* remains from Monte Culo de Maco had been dated exclusively. Had that been done, it would have been tempting to conclude that *Nesophontes* persisted—by association—to a point well within the post-Columbian period. Although we do not claim that the few dates reported here are dispositive, the onus is now on those who would continue to claim that island-shrews were able to persist in the West Indies long after 1500. We suspect that it would be hard to fashion either a direct-impact or a climate-based argument that could plausibly explain such rapid losses, although the hyperdisease theory recently proposed by MacPhee and Marx (1997) does allow for decadal-level collapses of populations challenged by introduced diseases (e.g., loss of native murines on Christmas Island [see also

TABLE 5
AMS ^{14}C Dates: *Nesophontes* from Cuba and Hispaniola

Species:	*N. micrus*	*N. paramicrus*	*N. hypomicrus*	*N. micrus*
Accession number:	(no number)	USNM 255780	AMNH (no number)	(no number)
Lab number:	Beta 115695	Beta 106566	Beta 104812	Beta 115696
Material	2 skulls	3 limb bones[a]	3 hemi-mandibles	skull fragments
Locality	Cueva Martin (Cuba)	shelter near Constanza (Hispaniola)	Cueva Jurg (Hispaniola)	Solapa La Jaula (Cuba)
Measured ^{14}C age, in rcyrbp	490 ± 50	590 ± 50	710 ± 50	770 ± 50
$^{13}C/^{12}C$ ratio	−18.9‰	−19.6‰	−19.8‰	−19.7‰
Conventional ^{14}C age, in rcyrbp (calibrated age intercept, in yr AD)[b]	590 ± 50 (cal-AD 1400)	680 ± 50 (cal-AD 1295)	790 ± 50 (cal-AD 1260)	850 ± 50 (cal-AD 1215)
Calibrated age range, 1 σ (68% probability), in yr AD	1310–1365 and 1375–1415	1285–1310 and 1355–1385	1220–1280	1170–1250
Calibrated age range, 2 σ (95% probability), in yr AD	1295–1430	1265–1400	1175–1295	1040–1275

[a] Specimens submitted were tibia-fibula, humerus, femur.
[b] Calibrated age ranges are not equivalent simply to "conventional" (^{13}C-adjusted) ^{14}C age ± 1 or 2 sigmas; the span of a given calibrated range depends on the specific shape of the calibration curve as it crosses confidence envelope around radiocarbon age intercept. Calibrated age intercept is the intercept of radiocarbon age with calibration curve, as reported by lab.

TABLE 6
AMS ^{14}C Dates: *Rattus rattus* from Hispaniola

Species:	*R. rattus*	*R. rattus*	*R. rattus*
Accession number:	USNM (no number)	USNM (no number)	USNM (no number)
Lab number:	Beta 108154	Beta 108152	Beta 108153
Material	femur	femur	femur
Locality	Monte Culo de Maco (Dominican Republic)	Monte Culo de Maco (Dominican Republic)	Monte Culo de Maco (Dominican Republic)
Measured ^{14}C age, in rcyrbp	220 ± 40	250 ± 30	440 ± 60
$^{13}C/^{12}C$ ratio	−19.5‰	−20.3‰	−22.6‰
Conventional ^{14}C age, in rcyrbp (calibrated age intercept, in yr AD)[b]	310 ± 40 (cal-AD 1640)	330 ± 30[a] (cal-AD 1525, 1560, 1630)	480 ± 60 (cal-AD 1435)
Calibrated age range, 1 σ (68% probability), in yr AD	1515–1585 and 1625–1650	1505–1595 and 1620–1640	1415–1455
Calibrated age range, 2 σ (95% probability), in yr AD	1475–1665	1475–1650	1395–1505 and 1595–1620

[a] Because of the shape of the calibration curve in this case, there are three possible intercepts of radiocarbon age with calibration curve.
[b] Calibrated age ranges are not equivalent simply to "conventional" (^{13}C-adjusted) ^{14}C age ± 1 or 2 sigmas; the span of a given calibrated range depends on the specific shape of the calibration curve as it crosses confidence envelope around radiocarbon age intercept. Calibrated age intercept is the intercept of radiocarbon age with calibration curve, as reported by lab.

Pickering and Norris, 1996]). In any case, if cause and effect were only briefly coupled in time, the chance of finding evidence of their contemporaneity is obviously very small (cf. Martin's [1984] argument concerning the unlikelihood of recovering archeological evidence of overkill in the North American end-Pleistocene extinctions). With further work, it is possible that the temporal gap between "last occurrence" of nesophontids and other extinct mammals and "first occurrence" of rats and other exotics will be narrowed, but it may never be closed empirically.

The other possibility is that the loss of the native fauna may have been due in some measure to introduced mammals, but that the introductions took place earlier than 1492. There is no evidence of which we are aware that Old World rats were introduced into North America when Vikings visited the northeast coast in the 11th century, and, even if there were, one would still have to explain how the rats got from the continent to the islands. A rather different scenario is that European vessels—carrying the usual unacknowledged cargo of murine fellow-travellers—occasionally reached the West Indies some decades or even centuries before Columbus' first voyage. Such a possibility has been repeatedly raised (e.g., Oldham, 1895; Batalha-Reis, 1897; Quinn, 1973), but has long been considered either wrong or untestable using the historian's conventional documentary sources (Morison, 1940; Skelton, 1995). However, if there were good chronometric evidence for the presence of *Rattus rattus* in the New World significantly before 1492, it would have to be considered in evaluating the possibility of pre-Columbian European contacts. As noted above, although one of the three dated rat femora from Monte Culo de Maco has an early 15th century intercept (cal-AD 1435), its calibration range overlaps the dates for the other two, which are later. Many more dates will be required to settle whether the date is just an anomaly or an actual signpost.

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